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Darwin's sexual selection theory – a forgotten idea

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Resumo A teoria de selecção sexual de Darwin é muito menos conhecida que a teoria de selecção natural e permaneceu praticamente desconhecida durante cerca de um século. Sendo hoje uma das teorias científicas mais prolíficas na biologia, é muito interessante, científica e epistemologicamente, entender porque permaneceu ignorada durante tanto tempo. Proponho que uma parte do seu abandono inicial teve, em parte, a ver com preconceitos sociais da época. Mas, porventura a razão mais significativa teve a ver com a dificuldade do conceito. Foi necessário um importante desenvolvimento teórico com a introdução de um pensamento populacional, que já estava presente em Darwin, e uma perspectiva de evolução centrada no gene, a par de desenvolvimentos formais, como a teoria de jogos, para se tornar possível desenvolverem e testar hipóteses que confirmassem a teoria. Nesta perspectiva, a visão de Darwin adquire uma dimensão ainda mais extraordinária.

Palavras-chave Darwin; selecção sexual; teoria científica; teoria de jogos; evolução.

Abstract Darwin's theory of sexual selection is much less known than his theory of natural selection, and remained mostly ignored for more than a century. Being today one of the most productive theories in biology, it is quite interesting to understand why it remained ignored for so long. I propose that part of its initial rejection had to do with social preconceptions. But, the most likely reason for being neglected had to do with the difficulty of the concept. A considerable theoretical development with the introduction of populational thinking, already present in Darwin, with a gene-centered view of evolution, and the development of new formal tools such as game theory were needed in order to put the theory under test. Under this perspective Darwin's feat seems even more remarkable.

Key words Darwin; sexual selection; scientific theory; game theory; evolution.

In 1871, Charles Darwin published one of his most important books: "*The descent of man and selection in relation to sex*" (Darwin, 1871). There he presents and justifies an extremely original theory that, in spite of its importance, became obscure or ignored for almost a century, with

one exception. That book is mostly known for the proposal of extending the concept of evolution by natural selection to our own species, a notion already implicit in the *Origin of species* (Darwin, 1859). Indeed, the only new scientific theory advanced in the book is Sexual Selection, which was criticized and above all ignored for a long time. After being badly received or ignored for so long, sexual selection theory became a central theory on modern evolutionary biology and behavioural ecology.

The theory of sexual selection attempted to solve an apparent paradox: how characteristics that reduce survival can evolve?

Why was such a powerful theory ignored for such a long time? Was it due to a Victorian puritan view of sex? Was it due to the difficulties of the theory? Was it due to the absence of appropriate tools to test it? I think that the causes are multiple including certainly social puritan attitudes of his time, as well as theoretical and more significantly lack of formal tools to allow to frame and test the theory. Indeed, I will attempt to show that other tools and approaches to evolutionary biology were needed before the idea could be tested.

The theory of sexual selection

When Darwin developed the theory of evolution by natural selection, he was not only proposing that organisms had not been created as they exist today, or in his time, but had evolved from less adapted ancestral forms. He was also advancing a mechanism to explain the evolution of adaptations. A mechanism providing a non-teleological explanation for the evolution of complex adapted traits in organisms (Mayr, 1991). The teleological explanations are well represented by the famous watch-watchmaker metaphor proposed by the bishop Paley. At that time, adaptations like duck interdigital membranes, or human thumb opposability, were difficult to explain without intentional guidance. Natural selection was such a mechanism. It provided explanation for the evolution of adaptive traits by selection, that is, by the increase of representatives carrying the genes that confer greater survival and reproductive advantage in relation to other members of the population. But the application of the theory raised new difficulties. If natural selection selects for the traits that confer greater survival to organisms, how can we explain the evolution of other traits that obviously hinder that survival, such as the brilliant colors of the body and size of the peacock's tail, or the bright coloration of pheasants, cardinals or guppies?

The explanation that Darwin (1871) proposed was not a simple one. He suggested that the peacock tail was selected, in spite of its reduction of male survival, because males with longer tails were preferred by females. And that the cost of survival was more than compensated by the increase in reproductive success. In modern genetic terms: if a gene responsible for longer tails has an increased fitness due to selection by females, in spite of the cost of survival, then it will increase its representation in the population and, eventually, will become fixed. That is, males will have longer tails even if longer tails decrease their survival.

Sexual selection was presented in two forms: intra-sexual selection and inter-sexual selection. The first would explain the evolution of arms for fighting between males, such as antlers, spurs or canines, for the exclusive or preferential access to females. The second was more complicated as it implied that females were attracted to males with exaggerated and costly traits, such as long tails, bright colors and other ornaments.

Following Darwin (1871: 398): *“the sexual struggle is of two kinds: in the one it is between the individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; while in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners.”*

Why females should prefer such male traits, was a question that Darwin attempted to answer with no data or examples to support his assertions. In his words *“What then are we to conclude from these facts and considerations? Does the male parade his charms with so much pomp and rivalry for no purpose? Are we not justified in believing that the female exerts a choice, and that she receives the addresses of the male who pleases her most? It is not probable that she consciously deliberates; but she is most excited or attracted by the most beautiful, or melodious, or gallant males”* (Darwin, 1871: 123). Darwin implies here that female's perceptive system is more excited by those traits. This also assumes no direct benefit to females.

Here Darwin attempts to avoid the problem of female choice as implying conscious deliberation. Not only we admit today that a choice mechanism can exist without requiring conscious thought as it is demonstrated in many examples (Krebs and Kacelnik, 1991). But that was a difficult conceptual jump at the time, when computers and software programs that can be used as analogy were yet to be invented. And, indeed, Wallace, Darwin's co-author

of natural selection, opposed the sexual selection theory precisely because he believed it implied conscious thought by females. He thus considered that the whole idea of ‘female choice’ was attributing judgment capacities of beauty to simple animals with no relevant cognitive capabilities such as a beetle.

Decades later Ronald Fisher (Fisher, 1915) developed a model for sexual selection through female choice in which he demonstrated that male traits such as peacock tails could evolve if male traits and female preference for exaggerated traits had a genetic basis and were inherited. Thus females could carry the gene for the preference and their sons the preferred trait. This would originate a runaway accelerating process as trait and preference would increase in a geometric proportion. This became known as the Fisherian runaway model of sexual selection (Andersson, 1994).

Fisher’s work was however a solitary exception and the whole subject remained untouched until the 1970’s. Only then the first experiments to test the possibility that females exerted a choice over male traits were done with unquestionable demonstration that female choice was a very powerful selective force acting on male traits (Andersson, 1982).

Besides Fisher’s runaway model, other sexual selection models to explain female choice were proposed in the 1970’s and 80’s, such as good genes models – good genes (Kodrick-Brown and Brown, 1984), handicap (Zahavi, 1975; Zahavi, 1977), healthy males (Hamilton and Zuk, 1982) – and sensory bias models (Ryan *et al.*, 1990). These models differ mostly on the causes for female choice. Good genes are indicator models, in the sense that the selected trait is a reliable signal of good genes or health. Sensory bias models assume a sensory exploitation of female’s sensory system by males.

Current relevance of sexual selection

Sexual selection is used today to explain many aspects of animal behaviour and the evolution of many characteristics. Mate guarding (Birkhead, 1979), extra-pair behaviour (Birkhead and Moller, 1998), ornaments (Petrie, 1994; Basolo, 1990), coloration (Hill and Montgomerie, 1994), song (Searcy and Yasukawa, 1996; Cardoso *et al.*, 2007), particular structures (Wilkinson and Reillo, 1994), or criptic female choice (Eberhard, 1996), both in animals and humans (Thornhill and Gangestad, 2006; Smith, 1984; Wedekind and Furi, 1997; Penton-Voak *et al.*, 2003).

We have pushed our understanding of the intricacy and complexity of nature far beyond we could think in the 1970's, in particular in the 'war of the sexes' and related issues. We now know that primate male's testis size is related to the degree of sperm competition and mating system in each species. We can predict mating system from male's relative testis size (Harcourt and Gardiner, 1994). *Drosophila* sperm can be 10 times larger than the male (3mm to 58mm), which is only susceptible of an explanation through sperm competition and sexual selection theory.

The whole field has been increasing very fast after the development of these models. For the most part, empirical tests, both in the laboratory and the field, have been conducted in order to determine which type of model was supported by the data. A survey on the ISI indexed journals indicates that sexual selection is increasing fast doubling the number of published articles per decade – 4500 in the 1990's and 10 000 in the 2000's.

Why was sexual selection neglected for so long? A difficult theory

The reception to the theory was cold. Although Darwin's contemporaries could accept that male-male competition does occur, and from it the evolution of weapons and size could follow, female choice was considered not acceptable. In the first place the whole idea that females could exert a choice collided with the relative irrelevant role that the male-centered Victorian English society attributed to women. It was a very male biased view of the two sexes capabilities: men considered that, in general, women were not capable of good judgment. Even Darwin reflects that view on his application of sexual selection theory to humans exposing several preconceptions and a male's European-centered view of sex in humans.

A second difficulty had to do with the idea of conscious choice. In the passage cited above, Darwin cautiously admits that 'it is not probable that' females 'consciously' deliberate. And again: "*for they have unconsciously, by the continued preference of the most beautiful males, rendered the peacock the most splendid of living birds*" (Darwin, 1871: 141). But what does it mean to be pleased or more excited as he proposes? What constitutes the basis of female choice? Consciousness is, then, at the center of the problem of female choice. Darwin was convinced that female choice occurred. But by what mechanism not requiring consciousness could ornament choice

be performed by female animals? Darwin thought that reason – conscious reasoning – is uniquely human: “*we can judge, as already remarked, of choice being exerted, only from the analogy of our own minds; and the mental powers of birds, if reason be excluded, do not fundamentally differ from ours*” (Darwin, 1871: 124). And, thus, uses expressions such as ‘struck’ – “*she is probably struck only by the general effect*” (Darwin, 1871: 123) – to suggest a different form of choice: a unconscious choice. Even so, at times he slipped into admitting conscious deliberation in animals, which makes it more difficult to support his view. When referring to the displays of pheasant males, Darwin goes into admitting consciousness to males: “*so that these birds seem conscious that they have little beauty to display*” (Darwin, 1871: 93). It was the issue of female consciousness that took Wallace to diverge from Darwin and not supporting his theory.

A third difficulty was that competition for his contemporaries was considered as taking place between species, not within species. This perspective was not fully understood for a long time and was responsible for important misconceptions on evolutionary thinking (Williams, 1966). But in the theory of sexual selection, competition takes place, not just within species, but also between the sexes. And this was not in the mind of naturalists of his time.

While intra-sexual selection was understandable since males better at competing with others were also evolving capacities to fight with competitors of other species or even predators, inter-sexual selection was a counterintuitive idea. In order for it to become more understandable and capable of generating new ideas and hypotheses to test it was necessary to develop a gene-centered view of evolution, and a theoretical tool capable of modeling different behaviours within a population of individuals, besides a populational thinking. The mathematical tools to deal with evolution in population were only developed through the works of Fisher, Haldane and Wright in the 1930-40’s. The theoretical tool for modeling of behaviour was game theory, introduced into biology by John Maynard-Smith (Maynard-Smith, 1982) in the 1970’s. And the gene-centered view, the greatest revolution in evolutionary thinking of the 2nd half of the 20th century, which changed entirely our view of nature and of evolution within it, was developed by evolutionary biologists such as G. C. Williams and William Hamilton (Williams, 1966; Hamilton, 1964).

Populational thinking

The theory of natural selection was put aside when the laws of Mendel were rediscovered in 1900, being replaced in the preferences of scientists by mutationism and other theories developed in the meanwhile (saltationism, orthogenesis). It was only when the neo-darwinian theory was developed joining natural selection with mendelian inheritance that the idea of sexual selection was approached by the brilliant Ronald Fisher. The modern synthesis, as it became known, demonstrated that when applying a populational thinking to genetics what really made sense was natural selection as a way to explain the gradual evolution of organisms' traits. Darwin thinking was really populational (Mayr, 1991) and this became a source of misunderstanding as most of his naturalist contemporaries and all philosophers of his time were thinking under a typological paradigm: species were seen as units, 'natural kinds', essential entities which did not intermix, not as composed by variable individuals which made up populations that were part of the intrinsic variability within each species. Fruit fly genetics allowed biologists to understand that each population of any species is constituted by different individuals, each carrying a different combination of genes (Mayr, 2001).

Individual and gene-centered view of nature

In the 1960's the evolutionary biologists George Williams (Williams, 1966), in the US, and William Hamilton (Hamilton, 1964), in the UK, reshaped our view of nature and of selection. They demonstrated that selection was not 'for the benefit' of species. It was instead 'for the benefit' of individuals or 'for the benefit' of the genes. This new understanding, that was developed and made more accessible by Richard Dawkins book 'the selfish gene' (Dawkins, 1976), was crucial for theory and research in the following years. This issue became known as the levels of selection or units of selection question (Lewontin, 1970; Guiddon and Gouyon, 1989; Sober, 1984). Presently, it is commonly accepted that evolution can take place at several levels simultaneously. However, the gene and phenotype levels are more effective at shaping evolutionary adaptations than the population or species levels (Williams, 1992; Mota, 1998). Thus, a gene-centered view of nature allowed us to understand the complexity of altruism in insects, the

existence of selfish DNA, or the conflict of interests between potential mates, or between the elements of a sexual population (Birkhead and Moller, 1998).

Theory of games and the understanding of behaviour evolution

In 1973, John Maynard-Smith (Maynard-Smith and Price, 1973) published a seminal paper that introduced a new mathematical tool in the research on evolution of behaviour: the theory of games. Developments of the theory allowed the understanding that alternative behaviours could exist within a single population, and that they could co-exist in a stable equilibrium without one selecting the other against (Maynard-Smith, 1982). This was another counterintuitive idea. The theory of games has been applied to a whole variety of behaviours whenever different strategies were involved (Gross, 1991; Clutton-Brock and Parker, 1995), as the cases of alternative mating strategies where satellite males, playing ‘females’ (Gross, 1984; Shuster and Wade, 1991; Taborsky, 1997; Oliveira *et al.*, 2001), attempt to obtain fertilizations (Parker, 1990; Lessells and Birkhead, 1990), or conflicts for resources in general. Sperm competition which is the result of sexual competition is generally considered to involve pre- and postcopulatory competition for fertilizations between males and females with interests that can be evolutionarily conflicting (Birkhead and Moller, 1998). Its development has been largely influenced by the application of theory of games to model possibilities.

The importance of mathematical models on population genetics and evolution: the example of the handicap theory

Sexual selection was an area in the study of behaviour where mathematical and theoretical models were first introduced prior to testing of the ideas. And this was precisely so because it was a counterintuitive idea. So it was necessary to have theoretical tools to address questions that could be tested and answered.

The example of the handicap theory proposed by Amotz Zahavi in 1975 to explain the evolution of handicaps like the peacock’s tail by a different mechanism is quite illustrative. Zahavi proposed that females were choosing those males because they were signaling their exceptional quality as they

could sustain such handicapping tails and still survive. Thus long tails were signals of high fitness, of good genes. John Maynard-Smith applied the theory of games to the idea and concluded that it could not work. And for some time it stayed like that. No attempts were made to test a hypothesis that could not work. But in 1990 Alan Grafen, another theoretical biologist, also applied the theory of games to the handicap model and showed that it could work in three different ways. This led to a strong research interest that is going on until today. Many cases of the handicap model have been found in nature (Harvey and Bradbury, 1991; Loyau *et al.*, 2007; Petrie, 1994; Moller, 1989; Moller and de Lope, 1994; Saino *et al.*, 1999).

How Darwin had such a foresight?

How was it possible that a 19th century naturalist, not provided with the theoretical and mathematical tools necessary for the development of these ideas, could have come to propose them? It is quite remarkable that Darwin could see so far.

I believe that some aspects of his thought were crucial to allow him to develop an explanation for the evolution of traits that, at a first look, were an exception to his natural selection theory.

A mechanistic view of nature

One of the most characteristic aspects of Darwin's thought is his mechanistic understanding of nature. For him, natural history had to work by the same kind of laws as the physical world. Not necessarily the same laws, but of the same nature. Any explanation for the complexity we find in natural world should avoid external inexplicable forces. This he makes clear in several places, like in the last sentences of the Origin where he invokes proximity to the laws of gravity explaining the cycling of the planet: "*There is a grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.*" (Darwin, 1859: 403).

A populational view of species

Unlike most of his contemporaries who were still thinking under a typological ‘fixed’ species concept, which originated in an essentialist perspective of species, Darwin had a real populational thinking. He realized that species had varieties, that there was a considerable variation. And he came to understand that this variation was the essential primary material for evolution to take place. Because he thought in population terms, he could think of selective forces affecting different types. In the same way as different populations of one species could diverge and, eventually, split into different species, also each sex could be subject to different selective forces. If not for his populational thinking it would be impossible for Darwin to arrive to his theory of sexual selection. *“the discovery of the importance of the individual became the cornerstone of Darwin’s theory on natural selection. It eventually resulted in the replacement of essentialism by population thinking, which emphasized the uniqueness of the individual and the critical role of individuality in evolution.”* (Mayr, 1991: 42).

An individual-centered view of selection

Competition was for Darwin first of all within a species. It was that competition that could drive the evolution of species adaptations, responding to their environmental challenges. But for his contemporaries and for a long period, competition was thought as between different species: between predators and prey, between competitors, between hosts and parasites. Very little attention was devoted to the competition within a species, which was clearly the center of Darwin’s explanation for natural selection as the main force for the evolution of organisms adaptations.

While celebrating Darwin’s 200th birth we should look into what has been the development of our knowledge and understanding of nature’s mechanisms and evolution in the last two centuries and be capable of putting in place the extraordinary revolution of thought that this exceptional scientist did.

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